EXPERIMENTS ON PHOTOPERIOD IN RELATION TO THE VEGETATIVE GROWTH OF PLANTS[1]

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Introduction

It has long been known that relative length of day and night effects the vegetative as well as the reproductive activity of plants. Since the appearance of the paper of GARNER and ALLARD (**7**) which first dealt with this subject, abundant factual material has accumulated relating to the influence of photoperiod on such varied processes as shoot elongation, leaf size, accumulation of dry weight and root growth (**6, 10**). It has been frequently, although not invariably, found that vegetative growth as measured by one or more of these criteria, is greater in long days than in short days irrespective of the reproductive behavior of the species in question. The promotive effect of long daily photoperiods on vegetative growth does not appear to be directly attributable to increased duration of CO_2 assimilation (**11**). Plants grown under conditions of long day made up of a short photoperiod of natural light supplemented by light of exceedingly low intensity exhibit the vegetative vigor typical of plants on a long day rather than that of plants on a short day regime (**13**).

It is known that the reproductive response of photoperiod sensitive plants is to be attributed to the production of a specific hormone (or hormones) in the leaves under conditions of suitable day length (**8, 9**). The production of this particular hormone or hormones would appear to depend on the length of day to which the leaves are subjected. It seems logical to inquire in how far the vegetative responses of plants to varying photoperiods are also attributable to the influence of day length on the production of the several hormones which regulate vegetative growth. In the present paper evidence will be presented to show that the production of vitamin B_1, a hormone for the growth of roots (**1**), is affected by the length of day to which the plant is subjected.

It is known that length of day exercises a profound effect on the extent of the root system in many species of plants. Thus WEAVER and HIMMEL (**12**) found that the root system is invariably more extensive under conditions of long photoperiod irrespective of whether the species of plant is long day, short day, or indeterminate with regard to flowering behavior. CRIST and STOUT (**5**) have also shown that the root system of plants grown under short photoperiod may be several times smaller than the root systems of similar plants grown under conditions of long photoperiod. These observa-

[1] Report of work done with the cooperation of the Works Progress Administration; Official Project no. 665-07-3-83, Work Project no. 9809.

tions suggest that the roots of plants grown under short photoperiod receive a limited amount of one or more of the substances required for root growth and supplied by the above ground portion of the plant.

Materials and methods

Plants were grown in the greenhouse in the manner previously described (**2**) in washed quartz sand contained in 2-gallon glazed crocks provided with drainage. They were supplied on alternate days with SHIVES R_2S_5 nutrient (including the minor elements Mn, Cu, Zn, B, Mo, and Fe) and the crocks flushed out with tap water on the intervening days. In each experiment one half of the plants were supplied with vitamin B_1 at the rate of 0.01 mg. per liter of nutrient solution. This concentration has been found in earlier experiments (**2**) to be non-toxic and promotive to the growth of many species of plants. Conditions of long photoperiod (18 to 20 hours) were maintained by means of supplementary illumination from Mazda lamps, approximately 80 foot-candles intensity at the leaf surface. Conditions of short photoperiod refer to a daily light period of 9 hours (8 A.M. to 5 P.M.).

In each experiment the vitamin B_1 content of the leaves (and in some cases of the roots) of the control and experimental plants was determined. This was done by means of the Phycomyces assay whose application to determination of vitamin B_1 in plant tissues has been described in detail in an earlier publication (**3**).

Experimental results

It is shown in table I that of the five species examined in the present experiments, every one contained less vitamin B_1 when cultured under a short photoperiod than when cultured under a long photoperiod. Of these spe-

TABLE I

SUMMARY OF DATA RELATIVE TO THE INFLUENCE OF PHOTOPERIOD ON VITAMIN B_1 CONTENT OF TOPS OF FIVE SPECIES OF PLANTS, GROWN IN SAND CULTURE AND ON LONG OR SHORT PHOTOPERIOD

SPECIES	FLOWERING PHOTO-PERIODIC BEHAVIOR	VITAMIN B_1 CONTENT			
		SHORT PHOTOPERIOD		LONG PHOTOPERIOD	
		PER GRAM DRY WEIGHT	PER SHOOT	PER GRAM DRY WEIGHT	PER SHOOT
		γ	γ	γ	γ
Xanthium	Short day	3.4	1.72	5.2	4.20
Cosmos	" "	4.9	0.26	5.1	0.38
Brassica alba	Long day	4.85	0.31	6.0	0.54
Brassica nigra	" "	2.95	0.14	3.9	0.22
Lycopersicum	Indeterminate	5.3	2.86	6.5	6.78

cies, two were short day with respect to production of flower hormones (that is, were "short day" plants), two were long day with respect to the production of this factor, and one was indeterminate. Nevertheless, all might be termed "long day" with respect to the production of vitamin B_1. It appears then justifiable to advance the working hypothesis that the vegetative growth responses of plants to photoperiod may be attributable in part to the decreased production of vitamin B_1 under conditions of short day. Support of this hypothesis is supplied by the fact that plants whose vitamin B_1 content is low because of maintenance under conditions of short photoperiod, do in certain cases respond more strongly to added vitamin than do parallel plants maintained under conditions of long photoperiod (table II, III).

TABLE II

EFFECT OF PHOTOPERIOD AND VITAMIN B_1 ON THE GROWTH OF XANTHIUM IN SAND CULTURE

	Short photoperiod					Long photoperiod				
	Dry weight per plant		Vitamin B_1 content		Number of plants	Dry weight per plant		Vitamin B_1 content		Number of plants
	Tops	Roots	Tops	Roots		Tops	Roots	Tops	Roots	
	mg.	*mg.*	γ	γ		*mg.*	*mg.*	γ	γ	
Control	510	57	1.72	0.19	47	810	133	4.20	0.69	36
Added vitamin B_1	855	105	3.76	0.46	37	1000	195	7.20	1.40	41

TABLE III

EFFECT OF PHOTOPERIOD AND VITAMIN B_1 ON THE GROWTH OF BRASSICA PLANTS IN SAND CULTURE. PLANTS HARVESTED SIX WEEKS AFTER PLANTING

Species	Short photoperiod		Long photoperiod	
	Dry weight per plant	Vitamin B_1 content	Dry weight per plant	Vitamin B_1 content
	mg.	γ	*mg.*	γ
B. alba				
Control	64	0.31	90	0.54
Added vitamin B_1	290	2.25	193	3.05
B. nigra				
Control	48	0.14	57	0.22
Added vitamin B_1	175	1.01	136	0.87

Xanthium pennsylvanicum (cocklebur) is a short day plant and flowers if maintained under daily photoperiods shorter than 15.5 hours. In the present experiments, the seedling plants were maintained for 3 weeks under conditions of long (18-hour) photoperiod. They were then divided into four equal lots and two lots transferred to conditions of a short (9-hour) photoperiod. One lot of those on each photoperiod received nutrient solution with added vitamin B_1; the other 2 lots received only nutrient solution. At the end of 4 weeks, when the plants were harvested, those maintained on long photoperiod were strictly vegetative while those maintained on short photoperiod possessed flowers and young fruits. Table II shows that of the control plants, those maintained under short photoperiod formed only 61 per cent. of the dry weight formed by those on long photoperiod, and that the dry weight of roots produced on short photoperiod was less than half that produced on long photoperiod. The plants maintained on short photoperiod and supplied with vitamin B_1, however, actually exceeded the long photoperiod control plants in total dry weight and produced 81 per cent. of the dry weight formed by the long photoperiod vitamin B_1 plants. The increased response to vitamin B_1 under conditions of short photoperiod is particularly striking in the case of the root system. The roots of the vitamin B_1 treated plants were almost 100 per cent. heavier than those of the control plants under conditions of short photoperiod and were only 44 per cent. heavier than the control roots under conditions of long photoperiod. Table II shows, then, that Xanthium plants on short photoperiod which contain relatively little vitamin B_1, respond more vigorously to addition of vitamin B_1 (with increased dry weight deposition) than do the plants on long photoperiod which contain relatively much vitamin B_1.

Brassica alba and *Brassica nigra* grown from unvernalized seed behave as long day plants. In the present experiments two lots of each species were maintained on long photoperiod and two lots of each species on short photoperiod. At the expiration of 6 weeks when the plants were harvested, those on long photoperiod were in full bloom, while those maintained continuously on short photoperiod were vegetative. Table III shows that with both species, less dry weight was accumulated (in the control series without vitamin B_1) under short photoperiod than was accumulated under long photoperiod. In each case also considerably less vitamin B_1 was found in the plants under short photoperiod than was found in the plants under long photoperiod. With both species the percentage increase in dry weight under the influence of vitamin B_1 is greater under short photoperiod than under long photoperiod.

It has been shown by ČAJLACHJAN and ŽDANOVA (4) that more auxin is produced by plants maintained under long photoperiods than by similar plants maintained under short photoperiods. In the present experiments it was found that Xanthium grown under long photoperiod contained considerable amounts of auxin,[2] but when grown under conditions of short

[2] Auxin determinations by Dr. J. VAN OVERBEEK.

photoperiod it contained no appreciable amount of auxin. The production of auxin by the plant appears to be affected by photoperiod just as is the production of vitamin B_1. It is to be expected that not only the formation of auxin and vitamin B_1 but also the formation of other growth factors may be affected by the daily photoperiod to which the plant is subjected. Under the conditions of the present experiments it would appear that production of vitamin B_1 is a particularly limiting factor in the case of Xanthium and of Brassica grown under conditions of short photoperiod. In other cases, other factors may be even more greatly affected than vitamin B_1. This may be the case with Cosmos whose response to added vitamin B_1 is less under short day conditions than under conditions of long day (table IV) and with tomato which does not respond to added vitamin B_1 either

TABLE IV

EFFECT OF PHOTOPERIOD AND VITAMIN B_1 ON THE GROWTH OF COSMOS GROWN IN SAND CULTURE. PLANTS HARVESTED FOUR WEEKS AFTER APPEARANCE OF FIRST LEAF

	SHORT PHOTOPERIOD				LONG PHOTOPERIOD			
	DRY WEIGHT PER PLANT		NUMBER OF PLANTS	VITAMIN B_1 PER SHOOT	DRY WEIGHT PER PLANT		NUMBER OF PLANTS	VITAMIN B_1 PER SHOOT
	TOPS	ROOTS			TOPS	ROOTS		
	mg.	*mg.*		γ	*mg.*	*mg.*		γ
Control	53	9.2	90	0.26	74.5	15.0	120	0.38
Added vitamin B_1	67	18.0	60	0.42	135.0	26.0	90	0.86

under long photoperiod or short photoperiod, although growth is decreased under the latter condition (table V).

TABLE V

EFFECT OF PHOTOPERIOD AND VITAMIN B_1 ON THE GROWTH OF TOMATO PLANTS IN SAND CULTURE. PLANTS HARVESTED THREE WEEKS AFTER APPEARANCE OF SECOND LEAF

	SHORT PHOTOPERIOD				LONG PHOTOPERIOD			
	DRY WEIGHT PER PLANT		NUMBER OF PLANTS	VITAMIN B_1 PER SHOOT	DRY WEIGHT PER PLANT		NUMBER OF PLANTS	VITAMIN B_1 PER SHOOT
	TOPS	ROOTS			TOPS	ROOTS		
	mg.	*mg.*		γ	*mg.*	*mg.*		γ
Control	540	70	10	2.86	1050	184	10	6.78
Added vitamin B_1	540	70	10	3.18	1260	248	10	5.67

Discussion

In an earlier paper (3) it has been shown that the leaves of the different species of plants vary greatly in their content of vitamin B_1. Different species presumably vary then in the amount of vitamin B_1 which they are able to synthesize. It has also been shown that of these various species, those which synthesize relatively large amounts of vitamin B_1 do not respond to the addition of this substance with increased growth, while those species which produce relatively little vitamin B_1 do respond to its addition with increased growth. The foregoing data show that with both Xanthium and Brassica, the amount of vitamin B_1 present in the plant is influenced by the photoperiod to which the plant is subjected. This is not unexpected in view of the fact that vitamin B_1 is formed by higher plants in the presence of light (**2**). The data also indicate that with Xanthium and Brassica the growth response to added vitamin is greater under conditions of short photoperiod (low vitamin B_1 synthesis) than it is under conditions of long photoperiod (higher vitamin B_1 synthesis). In the present experiments the vitamin B_1 content of the plant varies with the photoperiod; in the earlier experiments the vitamin B_1 content of the plant varied with the species but in both cases, relatively low vitamin B_1 content may be correlated with relatively large growth response to added vitamin B_1.

Summary

1. Plants of Xanthium, *Brassica alba, Brassica nigra,* Cosmos, and Lycopersicum all contain more vitamin B_1 when grown under conditions of long photoperiod (18 hours) than when grown under conditions of short photoperiod (9 hours).

2. Xanthium and Brassica respond to additions of vitamin B_1 more strikingly under the conditions of short photoperiod than under those of long photoperiod.

3. It is suggested that the effect of photoperiod on the vegetative growth of plants may be mediated by the effect of photoperiod upon the production, not only of vitamin B_1, but also on the production of other growth factors.

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